Assessing sources of error in comparative analyses of primate behavior: intraspecific variation in group size and the social brain hypothesis

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Abstract

Phylogenetic comparative methods have become standard for investigating evolutionary hypotheses, including in studies of human evolution. While these methods account for the non-independence of trait data due to phylogeny, they often fail to consider intraspecific variation, which may lead to biased or erroneous results. We assessed the degree to which intraspecific variation impacts the results of comparative analyses by investigating the “social brain” hypothesis, which has provided a framework for explaining complex cognition and large brains in humans. This hypothesis suggests that group life imposes a cognitive challenge, with species living in larger social groups having comparably larger neocortex ratios than those living in smaller groups. Primates, however, vary considerably in group size within species, a fact that has been ignored in previous analyses. When within-species variation in group size is high, the common practice of using a mean value to represent the species may be inappropriate. We conducted regression and resampling analyses to ascertain whether the relationship between neocortex ratio and group size across primate species persists after controlling for within-species variation in group size. We found that in a sample of 23 primates, 70% of the variation in group size was due to between-species variation. Controlling for within-species variation in group size did not affect the results of phylogenetic analyses, which continued to show a positive relationship between neocortex ratio and group size. Analyses restricted to non-monogamous primates revealed considerable intraspecific variation in group size, but the positive association between neocortex ratio and group size remained even after controlling for within-species variation in group size. Our findings suggest that the relationship between neocortex size and group size in primates is robust. In addition, our methods and associated computer code provide

46 a way to assess and account for intraspecific variation in other comparative analyses of primate
47 evolution.

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Introduction

Comparative analyses have played an important role in studies of primate and human evolution (Harvey and Pagel, 1991; Nunn, 2011). These analyses examine interspecific variation between different traits to infer adaptation, using species as the units of analysis. Because species are products of the evolutionary process and share traits via common descent, however, they cannot be considered as independent data points for statistical purposes (Felsenstein, 1985). As a consequence, evolutionary biologists have developed several procedures to control for phylogenetic non-independence (Nunn, 2011; Garamszegi, 2014a). The development and adoption of these techniques have increased the impact of comparative methods, but they make several important assumptions. One relatively neglected assumption concerns intraspecific variation. Specifically, most comparative methods assume that the entire range of variation in a trait of interest can be represented by a single data point, the species average (Garamszegi and Møller, 2010). Thus, variation around that value—due to measurement error, differences in sample size, or biologically relevant within-species variation—is typically ignored (Garamszegi, 2014b).

Ignoring within-species variation may lead to biases and spurious results in phylogenetic comparative analyses. For example, simulations revealed that failure to account for intraspecific variation can lead to a high Type I error rate (Harmon and Losos, 2005; Felsenstein, 2008; Silvestro et al., 2015). In cases where within-species variation exceeds between-species variation, it may be inappropriate to use mean values to represent an entire species in interspecific comparisons. This is of particular importance in studies of primates, given the considerable variability exhibited within species. This has long been noted as a concern in

comparative studies of primates. For example, Strier (2003: 5) stated that, “the compression of intraspecific variation in any behavioral trait into a single, species-specific value precludes interspecific comparisons...”. Similarly, Struhsaker (2000: 119) warned that there is a “need to better understand interpopulational and intraspecific variation [...]. Until this level of variation is understood and taken into consideration, broad interspecific comparisons and generalizations are misleading, if not counterproductive, in furthering the field of behavioral ecology”.

In addition, relying on small sample sizes may lead to poor quality data for traits that show high within-species variation (Garamszegi and Møller, 2010). Attention to the quality of data is a growing concern in comparative studies (Borries et al., 2013; Patterson et al., 2014). Sample size and variability are also salient issues in the study of hominin evolution and taxonomy. A small number of specimens, often quite variable due to biases in preservation (Behrensmeyer and Kidwell, 1985), may serve as the basis for inferences for an entire population (Wood and Lonergan, 2008). It is therefore crucial to interpret the hominin fossil record with methods that account for small sample size and accurately assess variation both within- and between-species.

Some comparative methods provide a way to incorporate intraspecific variation into analyses (Martins and Hansen, 1997; Ives et al., 2007; Felsenstein, 2008; Revell and Reynolds, 2012; Garamszegi, 2014b), but such analyses are rarely carried out in practice (Garamszegi and Møller, 2010). In many cases, data on intraspecific variation are unavailable. Even when such data are available, few studies have attempted to quantify the amounts of interspecific and intraspecific variation in traits being compared. The default procedure assumes that no within-species variation exists. The effect of ignoring intraspecific variation in comparative analyses has been studied for only a few systems, predominantly relying on simulated rather than actual data

(Harmon and Losos, 2005; Ives et al., 2007; Felsenstein, 2008; Hansen and Bartoszek, 2012).

Researchers have only recently begun to assess intraspecific variation in a comparative context

(e.g., Kamilar and Baden, 2014; Pap et al., 2015).

Group size in primates provides an example of the issues raised above and is the focus of this paper. Group size is a commonly employed variable in comparative studies of primates and other animals, as this trait is hypothesized to play a central role in the evolution of feeding ecology (Wrangham et al., 1993; Janson and Goldsmith, 1995), social relationships (Sterck et al., 1997; Lehmann et al., 2007), parasitism (Nunn et al., 2003; Rifkin et al., 2012), predator defense (Janson and Goldsmith, 1995; Hill and Lee, 1998), and complex cognition and large brains (Deaner et al., 2000; MacLean et al., 2013). Group size features prominently in tests of the social intelligence and social brain hypotheses, which suggest that, among primates, a selective premium is placed on the cognitive abilities of individuals who must manage relationships with multiple conspecifics in large groups (Chance and Mead, 1953/1988; Jolly, 1966; Humphrey, 1976; Byrne and Whiten, 1988; Dunbar, 1992). Support for the social brain hypothesis comes from several studies showing that neocortex size is positively correlated with group size across primate species (Sawaguchi and Kudo, 1990; Dunbar, 1992; Sawaguchi, 1992; Dunbar and Shultz, 2007). Understanding the evolution of large brains and complex cognition is a major question in the study of human evolution; thus, understanding the nuances of the analyses that underlie the social brain hypothesis is critically important for evolutionary anthropology.

The aforementioned studies used single values of group size to represent an entire species. This practice assumes that negligible variation exists in group size, yet this trait is known to vary considerably within primate species (Struhsaker, 2000; Mitani et al., 2012; Patterson et al., 2014; Strier et al., 2014). In chimpanzees, for example, communities range in size from approximately

20 to 200 individuals (e.g., Wilson et al., 2014), yet in one widely cited paper analyzing the relationship between neocortex size and group size, this variability is collapsed into a single value, 53.5 (Dunbar, 1992). While a species mean may accurately reflect the situation in solitary and socially monogamous primates where the only source of variation in “group” size is due to offspring being born and dispersing at maturity, a species mean is likely to conceal biologically meaningful variation for primates living in larger social groups (Kamilar and Baden, 2014; Patterson et al., 2014).

In this paper, we investigated the degree to which intraspecific variation in group size influences comparative tests of the social brain hypothesis in primates. First, we examine whether between-species variation in group size exceeds the variation found within species. To do this, we estimate within-species “repeatability” in group size in terms of the amount of interspecific variability in traits being analyzed in comparative studies relative to the total amount of variation in the data (Sokal and Rohlf, 1981; Nakagawa and Schielzeth, 2010). If repeatability is high (i.e., approximates 1), then most of the variation is due to differences between species. In contrast, when repeatability is low, considerable variation exists within species. When between-species repeatability is low, controlling for intraspecific variation becomes particularly important for comparative studies (Harmon and Losos, 2005).

Next, we implemented a regression method to control for intraspecific variability in the estimates of group size when analyzing the relationship between group size and neocortex ratio (Ives et al., 2007). Using a generalized linear model, this method uses as input the means for each species and the variance or standard errors around the mean. It then estimates parameters of the linear model, taking intraspecific variation into account.

Finally, we employed a resampling procedure to assess how different estimates of group size affect the relationship between neocortex ratio and group size. For this, we treated each within-species group size value as a potentially true value, using resampled values iteratively in statistical tests analyzing the association between neocortex ratio and group size. If within-species variation has negligible effects on the results of the comparative analysis, different group size values should produce little variance in the parameter estimates of different regression models. We also compared results from this analysis to a test of phylogenetic uncertainty, or error due to different probable phylogenies, as this is another source of variation that is more commonly assessed in comparative analyses (Pagel and Lutzoni, 2002; Arnold et al., 2010).

Materials and methods

Data collection

We collected brain size and group size values from the published literature for the same 26 monkey and ape species included in Dunbar's (1992) sample. Following Dunbar, we used the brain size data published by Stephan et al. (1981). Dunbar found the strongest correlation between group size and neocortex ratio, although other measures, including absolute neocortex volume, showed statistically significant positive relationships with group size. Continued debate exists about which brain variables are the best metrics to assay cognition for comparative research (Deaner et al., 2000; Healy and Rowe, 2007). Here, we followed Dunbar and colleagues by using the neocortex ratio, which is the volume of the neocortex divided by the rest of the brain, excluding the neocortex. Few samples of the neocortex sizes of individuals of different

primate species exist, and lacking estimates of within species variation in this measure, we focus only on variation in group size. We note, however, that the procedures that we implement could also be applied to analyses where both predictor and response variables vary within and between species, and the effect of measurement error (i.e., within-species variance) is different when present on the predictor or the response (Hansen and Bartoszek, 2012).

We employed data on group size from Patterson et al. (2014). These authors searched the primary literature for estimates of group size from studies in which subjects were habituated to human presence and where all individuals or their age-sex classes were known. Adopting these criteria may underestimate true variation within species; however, this procedure ensures the quality of the data and accuracy of group size estimates (Patterson et al., 2014). We found group size estimates for 23 species (range = 3–18 groups per species, median = 10 groups per species). For two taxa in our sample, *Alouatta* and *Cebus*, Stephan et al. (1981) only specified the genus, with no species identified for these data on brain size. For our analyses, we used group sizes for *Alouatta palliata* and *Cebus capucinus*.

Statistical analyses

Repeatability We calculated repeatability as the ratio of between-species variance relative to total variance (i.e., within- plus between-species variance). Group size values were log₁₀-transformed to meet the assumptions of the repeatability analyses for normally-distributed data (Nakagawa and Schielzeth, 2010). We conducted a linear mixed-effect model (LMM) to obtain variance components of repeatability (Nakagawa and Schielzeth, 2010). The first analysis employed the “lme4” package (Bates et al., 2013) in R (R Core Team, 2013), with log group size as the

response variable and species identity as a random factor. We then conducted a permutation test to determine whether the observed repeatability differed from a null model in which we reshuffled the group size data 1,000 times and calculated repeatability on each dataset. We compared our observed value to the tail of the distribution (see Supplementary Online Material [SOM 1]). To determine confidence intervals, we applied a parametric bootstrap in which data were simulated based on the estimated model parameters, and then the same model was fitted to estimate repeatability (sensu Efron and Tibshirani, 1993). This procedure was iterated 1,000 times, and the range of simulated repeatabilities was used to produce a confidence interval (2.5% and 97.5% quantiles).

Not all primates are expected to vary in group size to the same degree, and including species with different social systems may skew repeatability values. As mentioned previously, solitary and monogamous species have low within-species variability due to their small groups. Including these species in an analysis of repeatability will bias the result toward a high repeatability, i.e., higher between- relative to within-species variation, and may not be representative of within-species variation in primate group size. We therefore conducted a second repeatability analysis in which we excluded monogamous species.

Phylogenetic regression models We calculated species-specific trait values by averaging untransformed group size values, and conducted a phylogenetic generalized least squares (PGLS) regression analysis to assess the relationship between log neocortex ratio and log group size without accounting for within-species variance. We allowed the phylogenetic scaling factor (λ) to take a value at the maximum likelihood (Freckleton, 2009). To conduct this analysis, we used the ‘caper,’ ‘ape,’ and ‘nlme’ packages in R (Paradis et al., 2004; Orme et al., 2013; Pinheiro et

al., 2013; R Core Team, 2013). For all analyses assessing the relationship between group size and neocortex ratio, we defined neocortex ratio as the predictor variable and group size as the response variable, following previous tests of the social brain hypothesis (Dunbar, 1992; Dunbar and Shultz, 2007). As with repeatability analyses, we conducted two sets of regression analyses, the first including all 23 species and the second consisting of 17 group-living species that exclude socially monogamous ones.

Controlling for within-species variation We created measurement error models that adjust for within-species variation in group size through an error component of the PGLS model residuals. For this, we counted the number of samples of group size for each species and calculated their standard errors and variances. We log-transformed the variances and the means using the procedures described in Ives et al. (2007). The transformations assume that the values follow a log-normal distribution and are derived from the probability density function of that distribution (see also Quan and Zhang, 2003). Conducting such transformations is recommended for the statistical tests and also removes scale-dependence.

We compared the outputs of the measurement error model (i.e., model fit and parameter estimates) to the transformed PGLS model that only considers phylogeny and assumes that traits do not vary within species. Because the data are transformed, the parameters of the models controlling for measurement error are compared to models that used transformed data without controlling for measurement error, but are not comparable to the parameters from the original, untransformed PGLS model. We conducted analyses using the “MERegPHYSIG” package (Ives et al., 2007) in MATLAB. We conducted two sets of regression analyses, the first including all

23 species and the second consisting of 17 group-living species that exclude monogamous species.

Within-species resampling The measurement error method treats within-species variation as an error component in the linear model and attempts to recover the true mean values of the traits and the subsequent parameter estimates of the model. It is possible, however, that a single mean value is not an appropriate metric for a trait that is highly variable, and any single datum is just as accurate as any other for describing a species' trait. For certain traits, different populations of a single species may have very similar values, whereas for other traits, different populations of a single species may have wildly different values. A mean value may be appropriate for the former, but inappropriate for the latter.

With these concerns in mind, we implemented a resampling procedure as another way to incorporate within-species variation into comparative analyses. Here, we randomly chose one group size datum for each species from the available measurements and accepted this as the species-specific estimate (Mönkkönen and Martin, 2000). This resampling technique is similar to randomization procedures used by paleoanthropologists (e.g., Lockwood et al., 1996). This method does not account for the downward shift (attenuation bias) of the parameter estimates (e.g., slope) when within-species variation is taken into account (Freckleton, 2011; Garamszegi, 2014b). Nevertheless, this analysis is useful for assessing uncertainty in parameter estimates and visualizing the effect of within-species variation. Using this resampling scheme, we created 1,000 species-specific datasets that were subsequently analyzed by PGLS to investigate the relationship between group size and neocortex ratio. Some iterations encountered optimization errors, which relate to calculating the maximum likelihood of λ . Such optimization errors

(approximately 15) were ignored, and resampling continued until we had produced 1,000 models. To make inferences across these models, we determined the 95% confidence intervals of the derived intercepts and slopes and plotted the results. As with previous analyses, we conducted two sets of regression analyses, the first including all 23 species and the second consisting of 17 non-monogamous species.

Phylogenetic uncertainty Another potential source of error in comparative analyses is uncertainty in the phylogenetic relationships of species in the sample. Controlling for the evolutionary relationships of species addresses the problem of non-independence of data points. However, phylogenies themselves are not without error (Lutzoni et al., 2001; Pagel and Lutzoni, 2002; Arnold et al., 2010). We evaluated the effect of phylogenetic uncertainty by conducting a series of analyses where the evolutionary tree varies and the trait value of group size is held constant (Garamszegi and Mundry, 2014). We compared the results of these analyses to those derived from the resampling method examining the influence of within-species variation to assess which source of variation had a greater effect, trait uncertainty or phylogenetic uncertainty.

We assessed the influence of uncertainty in phylogenetic relationships by using 1,000 different phylogenetic trees from 10kTrees version 3, with the Wilson and Reeder (2005) taxonomy (Arnold et al., 2010). These trees were created using Bayesian phylogenetic methods, with trees thus sampled in proportion to their probability (Arnold et al., 2010). We then examined the relationship between neocortex ratio and group size using PGLS separately for each tree, resulting in 1,000 PGLS models. For each model, we allowed the phylogenetic scaling factor (λ) to take a value at its maximum likelihood (Freckleton, 2009). To make inferences from the large number of models, we applied model averaging that takes into account the different

degree of fit of the models to estimate regression slopes and intercepts (Garamszegi and Mundry, 2014). We also evaluated the regression outcomes graphically. We conducted the above analyses for all 23 species. For the subset of non-monogamous species, λ was close to 0, however. The impact of phylogeny on the regression models was negligible (see below), and thus, we did not investigate the effects of phylogenetic uncertainty for the non-monogamous subset of species.

To facilitate the application of these methods to other datasets, we provide the R code [SOM 1] and associated data files [SOM 2-3] for others to use. In addition, many of the analyses employed here are available as R code with instructions online: <http://www.mpcm-evolution.org> (Garamszegi, 2014a).

Results

Repeatability

Group size was variable within and between species (Fig. 1). Across all 23 primate species, between-species repeatability of group size can be considered moderate or high (linear mixed effect model [LMM] with parametric bootstrapping: $R = 0.733$, $p < 0.0001$, 95% CI = 0.565–0.825). Variance appeared to increase with increasing group size even after logarithmic transformation (Fig. 2). We assessed the relationship between mean values and variance in group size and found a weak but significant positive association, with larger groups exhibiting greater variance than smaller groups (PGLS regression: slope = 0.200 ± 0.077 , adjusted $R^2 = 0.207$, $p = 0.017$).

The relationship between the mean and variance in group size seemed to be driven partly by monogamous species that live in small groups and exhibit low variance. When monogamous species were excluded, we found no relationship between log-transformed mean group size and its variance (Fig. 2; PGLS regression: slope = 0.146 ± 0.159 , adjusted $R^2 = -0.010$, $p = 0.374$). We also conducted repeatability analyses after excluding monogamous species and found that between-species repeatability of group size was lower (LMM and parametric bootstrapping: $R = 0.477$, $p < 0.0001$, 95% CI = 0.275–0.628). Thus, greater within-species variability in group size exists in non-monogamous primates than in the wider primate sample; estimates of within- and between-species variation were similar in the non-monogamous species.

Phylogenetic regressions with and without controlling for intraspecific variation

Using our group size estimates for all 23 primate species (Patterson et al., 2014), we found a strong association between mean group size and neocortex ratio using standard phylogenetic comparative methods that did not control for intraspecific variation (Fig. 3; untransformed PGLS regression: slope = 4.081 ± 0.735 , $t = 5.551$, $R^2 = 0.575$, $p < 0.001$, $\lambda = 0.647$). These results are thus similar to those from previous analyses (Dunbar, 1992; Dunbar and Shultz, 2007). When monogamous species were excluded, a significant association between mean group size and neocortex ratio remained (untransformed PGLS regression: slope = 1.818 ± 0.734 , $t = 2.475$, $R^2 = 0.243$, $p = 0.026$, $\lambda = 0.001$).

In analyses that controlled for within-species variation, we again recovered a positive relationship between neocortex ratio and group size. The slopes derived from the models correcting for measurement error did not differ substantially from the model that did not

incorporate measurement error (Table 1). Within the subset of non-monogamous species, controlling for measurement error recovered a positive relationship, and the slopes derived from the models correcting for measurement error did not differ substantially from the equivalent model that ignored measurement error (Fig. 3). There was, however, additional noise, as there were moderate standard errors around the slope (Table 1).

Within-species resampling

How consistent is the relationship between group size and neocortex ratio using different measures of group size for each species? The resampling analysis produced a positive association between neocortex ratio and brain size (median slope = 3.314, 95% CI = 2.058–4.864; median intercept = 0.050, 95% CI = -0.531–0.434), with modest noise (Fig. 4a). In some cases, the slope was shallow, but the 95% confidence interval did not include zero.

The resampling analysis that included only non-monogamous species yielded similar results, although we documented considerable noise (Fig. 5). Regressions produced slopes that approached zero, and on rare occasions regressions produced negative slopes, but the 95% confidence interval excluded zero (median slope = 1.801, 95% CI = 0.269–3.456; median intercept = 0.650, 95% CI = 0.518–1.20). Taken together, these results reveal that, despite considerable within-species variation in group size, a positive correlation between group size and neocortex ratio persists.

Phylogenetic uncertainty

Phylogenetic uncertainty had weaker effects on the relationship between neocortex ratio and group size. Across all 23 species, model averaging indicated that the average slope was 4.148 with a 95% confidence interval of 2.697 to 5.599. The 95% confidence interval represented a wider range of slopes than actually occurred, as it is an “unconditional” confidence interval calculated based on the model averaged standard errors (Buckland et al., 1997; Burnham and Anderson, 2002; Mazerolle, 2013). Overall, the 1,000 regressions using different trees consistently produced similar findings (Fig. 4b).

Discussion

In addition to phylogenetic non-independence, within-species variation may influence the outcome of comparative analyses and should be considered in studies that investigate correlated trait evolution (Garamszegi, 2014b). Across a sample of primates, populations of the same species display variable group sizes. Substantially more variation, however, occurs between- rather than within-species. Specifically, we found that about 70% of the total variation was explained by interspecific variation. Controlling for within-species variation had little effect on the relationship between group size and neocortex ratio given this moderate repeatability. This finding is consistent with the results of a simulation study that found within-species variation has weak effects on the results of comparative analyses when at least 60% of the total variation in traits is explained by variation between species (Harmon and Losos, 2005).

In our analyses, incorporating within-species variation in group size had a negligible effect on regression models that investigated the relationship between neocortex ratio and group size. Similar results were derived from the resampling method. Resampling based on data from different populations created variable slope estimates, although these analyses recovered the positive relationship. The variability in slope estimates created by within-species variation was greater than that produced by phylogenetic uncertainty among the primate species in these analyses.

Some species vary more than others in group size. For example, solitary and monogamous species live in small groups, which vary little in size. Thus, these species are expected to have consistently small groups with little within-species variation. Group size is mediated by the mating and social system of the species: in polygynous and polygynandrous mating systems, sizeable influxes of males and/or females can occur over time. Monogamous species, however, do not generally allow immigrants to join their group, and their offspring disperse upon reaching maturity.

When we excluded monogamous species from the analysis, only 50% of the total variance in group size was explained by between-species differences. The lower within-species repeatability is likely driven by the exclusion of species that rarely vary, given the nature of pair bonded social systems. Using models that controlled for within-species variance recovered a positive association and produced similar slopes, although accounting for measurement error introduced considerable uncertainty. The resampling analysis that included only non-monogamous group-living primates revealed that slopes from regressions of group size on neocortex ratio ranged from 0.25 to 3.5. However, the slopes from models that controlled for

within-species variance did not differ significantly from the slopes in models that ignored within-species variance.

The finding that neocortex ratio is positively associated with group size after controlling for intraspecific variation in the latter trait in a sample of non-monogamous species is perhaps surprising. Our sample, however, was small, consisting of only 17 species. This small sample size may explain why, despite showing lower between-species repeatability than in the full sample, within-species variation failed to blur the relationship between brain size and group size. Additional analyses incorporating a larger sample of primates may shed additional light on whether within-species variation in traits influences the results of this and other comparative analyses.

One limitation of our study is that we only incorporated within-species variation in the response variable, as multiple measures of the neocortex size of individuals in different primate species are not available. This could further underestimate the true effect of within-species variation. Indeed, studies that have investigated brain size within and between species have documented considerable intraspecific variation (Sherwood et al., 2004). Ideally, analyses should incorporate variance in both the predictor and response variables. Similarly, alternative statistical approaches, such as those incorporating Bayesian probability and model selection, may add additional rigor to comparative studies, especially when data on intraspecific variation in the traits of interest are available (Revell and Reynolds, 2012).

We applied a diversity of approaches to investigate whether within-species variation influences the outcome of comparative studies, which has long been raised as a concern in studies of primate comparative biology (Struhsaker, 2000; Strier, 2003; Nunn, 2011). These approaches could be used in other comparative studies in evolutionary anthropology and human

evolution. For example, these analyses could be added to the repertoire of paleoanthropologists, who already use randomization and resampling procedures to make conclusions utilizing small samples or single specimens (e.g., Lockwood, 1999; Cardini and Elton, 2007; Cofran and DeSilva, 2015) and are increasingly incorporating phylogenetic comparative methods in their research (e.g., Pontzer et al., 2014; Gonzales et al., 2015; Pampush, 2015; Russo, 2016).

We focused on group size, which is a key variable in comparative studies inferring the evolution of large brains (Sawaguchi and Kudo, 1990; Dunbar, 1992; Sawaguchi, 1992; Dunbar and Shultz, 2007) . Understanding encephalization in primates and humans is a major question in evolutionary anthropology, and the social brain hypothesis has provided a powerful framework for understanding brain evolution. Our findings indicate that the wide range of group size values present in several primate species does not erase the association between group size and neocortex ratio across primates. This association is recovered despite a high degree of within-species variation in group size among non-monogamous primates. Thus, among monkeys and apes, species that tend to live in larger groups also tend to have relatively larger neocortices, affirming the relationship between brain size and sociality in primates. This lends support to the hypothesis that sociality, not just ecology, has been an important factor in the evolution of brain size and cognitive abilities among primates, including humans.

Given the potential impact of intraspecific variation, researchers who have previously conducted comparative analyses utilizing species averages of group size may be tempted to breathe a sigh of relief. However, our results should not imply that within-species variation can be ignored. Whether between-species variation exceeds within-species variation will be influenced by the taxa and traits under consideration. Hence, when the data exist, analyses such as those presented here should be performed. In future studies, when repeatability is low,

methods incorporating within-species variation should be employed. Including within-species variation in phylogenetic comparative analyses can reduce biases created by ignoring known variance and increase confidence about parameter estimates. Additional research investigating other sources of error that can arise in comparative studies is required and will ultimately strengthen the conclusions from these analyses. Finally, additional data on neocortex size and comparative analyses of brain structures, group size, and other variables, including ecological traits, will further elucidate the forces associated with the evolution of large brains.

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References

- Arnold, C., Matthews, L.J., Nunn, C.L., 2010. The 10kTrees website: a new online resource for primate phylogeny. *Evol. Anthropol.* 19, 114–118.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2013. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-5.
- Behrensmeyer, A.K., Kidwell, S.M., 1985. Taphonomy's contributions to paleobiology. *Paleobiology* 11, 105–119.
- Borries, C., Gordon, A.D., Koenig, A., 2013. Beware of primate life history data: a plea for data standards and a repository. *PLoS ONE* 8, e67200.
- Buckland, S.T., Burnham, K.P., Augustin, N.H., 1997. Model selection: an integral part of inference. *Biometrics* 53, 603–618.
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer, New York.
- Byrne, R.W., Whiten, A.W., 1988. Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes, and humans. Clarendon Press, Oxford.
- Cardini, A., Elton, S., 2007. Sample size and sampling error in geometric morphometric studies of size and shape. *Zoomorphology* 126, 121–134.
- Chance, M.R.A., Mead, A.P., 1953/1988. Social behaviour and primate evolution. In: Byrne, R.W., Whiten, A.W. (Eds.), Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes, and humans. Clarendon Press, Oxford, pp. 34-49.
- Cofran, Z., DeSilva, J.M., 2015. A neonatal perspective on *Homo erectus* brain growth. *J. Hum. Evol.* 81, 41–47.

501 Deaner, R.O., Nunn, C.L., van Schaik, C.P., 2000. Comparative tests of primate cognition:
 502 Different scaling methods produce different results. *Brain Behav. and Evol.* 55, 44–52.
 503 Dunbar, R.I.M., 1992. Neocortex size as a constraint on group size in primates. *J. Hum. Evol.* 22,
 504 469–493.
 505 Dunbar, R.I.M., Shultz, S., 2007. Evolution in the social brain. *Science* 317, 1344–1347.
 506 Efron, B., Tibshirani, R.J., 1993. An introduction to the bootstrap. *Monographs on Statistics and*
 507 *Applied Probability* 57. Chapman & Hall, New York.
 508 Felsenstein, J., 1985. Phylogenies and the comparative method. *Amer. Nat.* 125, 1–15.
 509 Felsenstein, J., 2008. Comparative methods with sampling error and within-species variation:
 510 contrasts revisited and revised. *Amer. Nat.* 171, 713–725.
 511 Freckleton, R.P., 2009. The seven deadly sins of comparative analysis. *J. Evol. Bio.* 22, 1367–
 512 1375.
 513 Freckleton, R.P., 2011. Dealing with collinearity in behavioural and ecological data: model
 514 averaging and the problems of measurement error. *Behav. and Brain Sci.* 65, 91–101.
 515 Garamszegi, L.Z., 2014a. Modern phylogenetic comparative methods and their application in
 516 evolutionary biology. Springer-Verlag, Berlin.
 517 Garamszegi, L.Z., 2014b. Uncertainties due to within-species variation in comparative studies:
 518 measurement errors and statistical weights. In: Garamszegi, L.Z. (Ed.), *Modern*
 519 *phylogenetic comparative methods and their application in evolutionary biology.*
 520 Springer-Verlag, Berlin, pp. 157–199.
 521 Garamszegi, L.Z., Møller, A.P., 2010. Effects of sample size and intraspecific variation in
 522 phylogenetic comparative studies: a meta-analytic review. *Biol Rev.* 85, 797–805.

523 Garamszegi, L.Z., Mundry, R., 2014. Multimodel-inference in comparative analyses. In:
 524 Garamszegi, L.Z. (Ed.), Modern phylogenetic comparative methods and their application
 525 in evolutionary biology. Springer-Verlag, Berlin.
 526 Gonzales, L.A., Benefit, B.R., McCrossin, M.L., Spoor, F., 2015. Cerebral complexity preceded
 527 enlarged brain size and reduced olfactory bulbs in Old World monkeys. *Nature Comm.* 6,
 528 7580.
 529 Hansen, T.F., Bartoszek, K., 2012. Interpreting the evolutionary regression: The Interplay
 530 between observational and biological errors in phylogenetic comparative studies. *Syst.*
 531 *Biol.* 61, 413–425.
 532 Harmon, L.J., Losos, J.B., 2005. The effect of intraspecific sample size on type I and type II
 533 error rates in comparative studies. *Evolution* 59, 2705–2710.
 534 Harvey, P., Pagel, M., 1991. The comparative method in evolutionary biology. Oxford
 535 University Press, Oxford.
 536 Healy, S.D., Rowe, C., 2007. A critique of comparative studies of brain size. *Proc. R. Soc. B* 274,
 537 453–464.
 538 Hill, R.A., Lee, P.C., 1998. Predation risk as an influence on group size in cercopithecoid
 539 primates: implications for social structure. *J Zool.* 245, 447–456.
 540 Humphrey, N.K., 1976. The social function of intellect. In: Bateson, P., Hinde, R. (Eds.),
 541 Growing points in ethology. Cambridge University Press, Cambridge, pp. 303–317.
 542 Ives, A.R., Midford, P.E., Garland, T., 2007. Within-species variation and measurement error in
 543 phylogenetic comparative methods. *Syst. Biol.* 56, 252–270.
 544 Janson, C.H., Goldsmith, M.L., 1995. Predicting group size in primates: foraging costs and
 545 predation risks. *Behav. Ecol.* 6, 326–336.

546 Jolly, A., 1966. Lemur social behavior and primate intelligence. *Science* 153, 501–506.

547 Kamilar, J.M., Baden, A.L., 2014. What drives flexibility in primate social organization? *Behav.*
548 *Ecol. Sociobiol.* 68, 1677–1692.

549 Lehmann, J., Korstjens, A.H., Dunbar, R.I.M., 2007. Group size, grooming and social cohesion
550 in primates. *Anim. Behav.* 74, 1617–1629.

551 Lockwood, C.A., 1999. Sexual dimorphism in the face of *Australopithecus africanus*. *Amer. J*
552 *Phys. Anth.* 108, 97–127.

553 Lockwood, C.A., Richmond, B.G., Jungers, W.L., 1996. Randomization procedures and sexual
554 dimorphism in *Australopithecus afarensis*. *J. Hum. Evol.* 31, 537–548.

555 Lutzoni, F., Pagel, M., Reeb, V., 2001. Major fungal lineages are derived from lichen symbiotic
556 ancestors. *Nature* 411, 937–940.

557 MacLean, E.L., Sandel, A.A., Bray, J., Oldenkamp, R.E., Reddy, R.B., Hare, B.A., 2013. Group
558 size predicts social but not nonsocial cognition in lemurs. *PLoS ONE* 8, e66359.

559 Martins, E.P., Hansen, T.F., 1997. Phylogenies and the comparative method: a general approach
560 to incorporating phylogenetic information into the analysis of interspecific data. *Amer.*
561 *Nat.* 149, 646–667.

562 Mazerolle, M.J., 2013. AICcmodavg: model selection and multimodel inference based on
563 (Q)AIC(c). R package version 1.35.

564 Mitani, J.C., Call, J., Kappeler, P.M., Palombit, R.A., Silk, J.B., 2012. The evolution of primate
565 societies. University of Chicago Press, Chicago.

566 Mönkkönen, M., Martin, T.E., 2000. Sensitivity of comparative analyses to population variation
567 in trait values: clutch size and cavity excavation tendencies. *J. Avian Biol.* 31, 576–579.

568 Nakagawa, S., Schielzeth, H., 2010. Repeatability for Gaussian and non-Gaussian data: a
 569 practical guide for biologists. *Biol. Rev.* 85, 935–956.
 570 Nunn, C.L., 2011. The comparative approach in evolutionary anthropology and biology.
 571 University of Chicago Press, Chicago.
 572 Nunn, C.L., Altizer, S., Jones, K.E., Sechrest, W., 2003. Comparative tests of parasite species
 573 richness in primates. *Amer. Nat.* 162, 597–614.
 574 Orme, D., Freckleton, R.P., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., Pearse, W., 2013.
 575 caper: comparative analyses of phylogenetics and evolution in R. R package version 0.5.2.
 576 Pagel, M., Lutzoni, F., 2002. Accounting for phylogenetic uncertainty in comparative studies of
 577 evolution and adaptation. In: Lässig, M., Valleriani, A. (Eds.), *Biological Evolution and*
 578 *Statistical Physics*. Springer Berlin Heidelberg, pp. 148–161.
 579 Pampush, J.D., 2015. Selection played a role in the evolution of the human chin. *J. Hum. Evol.*
 580 82, 127–136.
 581 Pap, P.L., Osváth, G., Sándor, K., Vincze, O., Bárbos, L., Marton, A., Nudds, R.L., Vágási, C.I.,
 582 2015. Interspecific variation in the structural properties of flight feathers in birds
 583 indicates adaptation to flight requirements and habitat. *Funct. Ecol.* 29, 746–757.
 584 Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R
 585 language. *Bioinformatics* 20, 289–290.
 586 Patterson, S.K., Sandel, A.A., Miller, J.A., Mitani, J.C., 2014. Data quality and the comparative
 587 method: the case of primate group size. *Int. J. Primatol.* 35, 990–1003.
 588 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2013. nlme: Linear and Nonlinear
 589 Mixed Effects Models.

590 Pontzer, H., Raichlen, D.A., Gordon, A.D., Schroepfer-Walker, K.K., Hare, B., O'Neill, M.C.,
 591 Muldoon, K.M., Dunsworth, H.M., Wood, B.M., Isler, K., Burkart, J., Irwin, M.,
 592 Shumaker, R.W., Lonsdorf, E.V., Ross, S.R., 2014. Primate energy expenditure and life
 593 history. *Proc. Natl. Acad. Sci. USA* 111, 1433–1437.

594 Quan, H., Zhang, J., 2003. Estimate of standard deviation for a log-transformed variable using
 595 arithmetic means and standard deviations. *Stat. Med.* 22, 2723–2736.

596 R Core Team, 2013. R: A language and environment for statistical computing, Vienna, Austria.

597 Revell, L.J., Reynolds, R.G., 2012. A new Bayesian method for fitting evolutionary models to
 598 comparative data with intraspecific variation. *Evolution* 66, 2697–2707.

599 Rifkin, J.L., Nunn, C.L., Garamszegi, L.Z., 2012. Do animals living in larger groups experience
 600 greater parasitism? A meta-analysis. *Amer. Nat.* 180, 70–82.

601 Russo, G.A., 2016. Comparative sacral morphology and the reconstructed tail lengths of five
 602 extinct primates: *Proconsul heseloni*, *Epipliopithecus vindobonensis*, *Archaeolemur*
 603 *edwardsi*, *Megaladapis grandidieri*, and *Palaeopropithecus kelyus*. *J. Hum. Evol.* 90,
 604 135–162.

605 Sawaguchi, T., 1992. The size of the neocortex in relation to ecology and social structure in
 606 monkeys and apes. *Folia Primatol.* 58, 131–145.

607 Sawaguchi, T., Kudo, H., 1990. Neocortical development and social structure in primates.
 608 *Primates* 31, 283–289.

609 Sherwood, C.C., Cranfield, M.R., Mehlman, P.T., Lilly, A.A., Garbe, J.A.L., Whittier, C.A.,
 610 Nutter, F.B., Rein, T.R., Bruner, H.J., Holloway, R.L., Tang, C.Y., Naidich, T.P., Delman,
 611 B.N., Steklis, H.D., Erwin, J.M., Hof, P.R., 2004. Brain structure variation in great apes,

612 with attention to the mountain gorilla (*Gorilla beringei beringei*). Am. J. Primatol. 63,
613 149–164.

614 Silvestro, D., Kostikova, A., Litsios, G., Pearman, P.B., Salamin, N., 2015. Measurement errors
615 should always be incorporated in phylogenetic comparative analysis. Methods Ecol. Evol.
616 6, 340–346.

617 Sokal, R.R., Rohlf, F.J., 1981. Biometry: the principles and practice of statistics in biological
618 research, 2nd ed. W.H. Freeman & Company, New York.

619 Stephan, H., Frahm, H., Baron, G., 1981. New and revised data on volumes of brain structures in
620 insectivores and primates. Folia Primatol. 35, 1–29.

621 Sterck, E.H., Watts, D.P., van Schaik, C.P., 1997. The evolution of female social relationships in
622 nonhuman primates. Behav. Ecol. Sociobiol. 41, 291–309.

623 Strier, K.B., 2003. Primatology comes of age: 2002 AAPA Luncheon address. Amer. J. Phys.
624 Anthropol. 122, 2–13.

625 Strier, K.B., Lee, P.C., Ives, A.R., 2014. Behavioral flexibility and the evolution of primate
626 social states. PLoS ONE 9, e114099.

627 Struhsaker, T.T., 2000. Variation in adult sex ratios of red colobus monkey social groups:
628 implications for interspecific comparisons. In: Kappeler, P.M. (Ed.), Primate Males.
629 Cambridge University Press, Cambridge, pp. 108–119.

630 Wilson, D.E., Reeder, D.M., 2005. Mammal species of the world: a taxonomic and geographic
631 reference, 3rd ed. Johns Hopkins University Press, Baltimore.

632 Wilson, M.L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I.C., Hashimoto, C., Hobaiter, C.L.,
633 Hohmann, G., Itoh, N., Koops, K., Lloyd, J.N., Matsuzawa, T., Mitani, J.C., Mjungu,
634 D.C., Morgan, D., Muller, M.N., Mundry, R., Nakamura, M., Pruett, J., Pusey, A.E.,

Riedel, J., Sanz, C., Schel, A.M., Simmons, N., Waller, M., Watts, D.P., White, F., Wittig,
R.M., Zuberbuhler, K., Wrangham, R.W., 2014. Lethal aggression in *Pan* is better
explained by adaptive strategies than human impacts. *Nature* 513, 414–417.

Wood, B., Lonergan, N., 2008. The hominin fossil record: taxa, grades and clades. *J. Anat.* 212,
354–376.

Wrangham, R.W., Gittleman, J.L., Chapman, C.A., 1993. Constraints on group size in primates
and carnivores: population density and day-range as assays of exploitation competition.
Behav. Ecol. Sociobiol. 32, 199–209.

Figure legends

Figure 1. Within- and between-species variation in group size across sample of 23 primates. The boxplot shows the median and spread of data: the box represents the 25th and 75th percentiles, whiskers represent minimums and maximums relative to the interquartile range, and circles represent outliers.

Figure 2. The relationship between average primate group size and its variance. Gray dots = monogamous species, black dots = non-monogamous species, solid line = significant relationship for all 23 species, dotted line = non-significant relationship between group size and variance among non-monogamous species.

Figure 3. The relationship between neocortex ratio versus mean group size. Gray dots = monogamous species, black dots = non-monogamous species, light gray circles = group size transformed variance, black lines = all 23 species, gray lines = non-monogamous species only, solid lines = transformed PGLS regression with no measurement error, dashed lines = Ives et al. (2007) max. likelihood model.

Figure 4. Evaluating the effects of within species variation in group size and phylogenetic uncertainty. (a) Within species variation in group size. The relationship between group size and neocortex ratio is shown after resampling species-specific group size values using a consensus tree (1,000 regressions). (b) Phylogenetic uncertainty. The relationship between group size and neocortex ratio is shown using 1,000 different probable phylogenies with mean group size values.

680 Gray lines = individual regressions, dashed lines = regression based on mean group size values
681 and the consensus tree.

682

683 **Figure 5.** The relationship between group size and neocortex ratio in a sample of 17 non-
684 monogamous primate species. Results of resampling species-specific group size values with a
685 consensus tree (1,000 regressions) are shown. Gray lines = individual regressions, dashed line =
686 regression based on mean group size values and the consensus tree.

Table 1. Coefficients and standard errors of models examining the relationship between neocortex ratio and group size.^a

	All species		Group-living (monogamous excluded)	
	Slope	Intercept	Slope	Intercept
Without considering within-species variance	10.625	-1.00	8.323	0.010
With approx. variance (estimated generalized least-square)	10.625 ± 1.634	-1.013 ± 0.672	8.323 ± 2.277	-0.003 ± 0.947
With approx. variance (maximum likelihood)	10.332 ± 1.549	-0.923 ± 0.622	7.822 ± 2.026	0.160 ± 0.829

^a Values are shown for models ignoring variance (top model) and those incorporating within-species variance (lower two models, based on Ives et al., 2007).

Figure 1

Figure 2

Figure 3

Figure 4

A. Within-species Resampling

B. Phylogenetic Uncertainty

Figure 5

Within-species Resampling